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THE SPATIAL DISTRIBUTION OF ERRORS MADE BY RATS IN HEBB-WILLIAMS TYPE MAZES IN
RELATION TO THE SPATIAL PROPERTIES OF THE BLIND ALLEYS

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ABSTRACT

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The various configurations in series of Hebb-Williams type of mazes, which are used to measure problem solving behaviour in rats, differ markedly in structure. The relationship between error behaviour and spatial maze structure in control rats tested in a number of pharmacological experiments is described in this paper. The spatial structure of error behaviour of rats was found to correlate with maze structure. Knowledge of these correlations can be used to predict error patterns in new mazes. Furthermore, aspecific experience acquired by running in a number of different configurations, affected error behaviour in a particular test configuration. This effect of aspecific experience was different from that of specific experience acquired in the same test configuration. In studies investigating effects of (e.g. pharmacological) treatments on maze behaviour of rats, changes in the structure of errors may be useful to determine the nature of the behavioural alterations.

Key words: rat, food reward, Hebb-Williams maze, spatial error distribution, blind alley characteristics, experience, problem solving strategy

GENERAL INTRODUCTION

Hebb-Williams type problem solving tests are conventionally employed to measure effects of various kinds of manipulations (e.g. brain lesions, environmental rearing conditions, endocrine manipulations, pharmacological and toxicological treatment) on cognitive performance of laboratory rats. Such a test consists of a series of different maze configurations constructed by placing barriers in various ways in a square box. The configurations in each series have been designed with the aim to measure a mixture of cognitive abilities. Therefore, a considerable variation in spatial structure and difficulty level was introduced. The animals are trained and tested in a series of sessions with different configurations. The first few sessions serve for habituation and pretraining: the animals are trained to perform the general task in a number of simple

configurations, i.e. to go from the start box to the goal box to obtain food reward. Subsequently they are tested in a series of more complicated configurations.

There are different series of configurations. After the original set of Hebb and Williams (1946), two others were developed by Rabinovitch and Rosvold (1951) and Davenport et al. (1970). The Rabinovitch-Rosvold series consists of asymmetrical test configurations. The rat is allowed to run in only one direction through the maze. A new trial starts with placing the rat back in the start box. The Davenport series has symmetrical test configurations. Therefore, the rat can be left in the maze and run back and forth without the intervention of the experimenter. The rats are trained to run in two directions between two boxes which alternatively function as start- and goal box, the routes are identical in both directions.

From research in various types of mazes (e.g. composite T-mazes, Dashiell mazes) it is known that rat behaviour in mazes is structured. Exploration (Glanzer, 1961; Uster et al., 1976) as well as e.g. food rewarded behaviour (Tryon, 1940a) in mazes correlate with spatial characteristics of the maze. The degree of difficulty of a maze configuration depends not only on the number of alleys, but also on certain properties of the alleys: learning to enter or not enter is much more difficult for some of the alleys than for others. This relationship between spatial maze characteristics and the structure of maze learning in rats has been studied by several investigators in the first half of this century (Buel, 1935, Tryon, 1940a). Because spatial locomotor patterns of rats can be altered by pharmacological treatment (Bättig et al., 1976; Flicker and Geyer, 1982; Martin et al., 1981, 1982), the spatial structure of error patterns in food rewarded maze tests probably can also be affected by drugs.

Although some investigators have analyzed the behavioural patterns to interpret the effects of brain lesions on learning of Hebb-Williams mazes (Kimble and BreMiller, 1981; Kimble et al., 1982), a clear description of the spatial error behaviour of rats in Hebb-Williams mazes is not available. In this paper we present a description of the error behaviour of saline treated control rats taken from a number of pharmacological experiments in the series of 12 Davenport configurations, and show the correlation of this behaviour with structural characteristics of the mazes. In addition, effects of different kinds of experience on error behaviour are described.

I. DESCRIPTION OF THE ERROR PATTERNS

The data presented by Davenport et al. (1970) show that there is a large variation in the number of errors made in the various configurations in their problem solving test. This may, at least partly, be caused by the variation in

the difficulty levels of the blind alleys, similar to that shown by Tryon (1940a, b) for composite T-mazes. In this section the error patterns of rats in the different Davenport configurations are shown.

MATERIAL AND METHODS

Animals

Naive male Wistar rats of an inbred strain (CPB-TNO, Zeist, The Netherlands) were housed in groups of 3 or 4 per cage under a controlled light-dark schedule (light on between 6.00 and 20.00 h). Water was supplied ad libitum. The initial body weights varied between 140 and 190 g (approximate age: 6-8 weeks). Data of 25 placebo treated (i.e. a 0.5 ml subcutaneous saline injection one hour before each test session) control rats from three pharmacological experiments were pooled.

Food deprivation schedule

Immediately after the habituation session the food was taken away. Food was supplied after each pretraining or test session for a period of 90 minutes, immediately after the return of the last rat to the cage. From Friday until Sunday morning ad libitum food was given, training and testing were discontinued in the weekend. On this deprivation scheme the body weight of the animals was reduced to about 80-90 %.

Apparatus

The maze was constructed after the description of Davenport et al. (1970) from Perspex, with a red bottom and black walls, barriers and doors. The field was 60 x 60 cm, to which at two opposite corners start/goal boxes (end boxes) of 18 x 38 cm were fixed. All walls were 20 cm high. Sliding doors separated the two boxes at the corners from the field. In the field, barriers of 10 cm high could be fixed to the bottom by means of pins fitting into holes. The whole apparatus was covered by wire mesh right above the barriers in the field, and right above the walls of the end boxes. In each end box the food pellets could be dropped via a vertically hanging metal tube into a white porcelain dish (diameter 5 cm).

The only light source in the experimental room was a 40 W lamp fixed at a distance of 1 m above the centre of the bottom of the field of the maze.

Behavioral training and testing procedures

The procedure was divided into three phases: habituation, pretraining and testing.

Habituation:

On day one the undeprived rats had the opportunity to explore the maze without barriers during two sessions of 5 min each. They started once from each of the two end boxes with an intertrial interval of at least one hour. Food pellets were available in the end boxes.

Pretraining and testing:

The deprived rats had one session a day, each day in a new configuration. The configurations were P1-P5 in the pretraining phase and T1-T12 in the testing phase (fig. 1).

During pretraining and testing each session consisted of 12 trials in alternating directions. The two end boxes functioned alternatively as goal box and start box. The first trial always started in same end box. The rat was placed into the compartment facing away from the sliding door, which was opened 5 sec later. Intertrial intervals lasted 15 sec, except for the first few pretraining sessions, when the animals were allowed more time to consume the food reward. In this way the two end boxes functioned alternatively as goal box and start box. Reward consisted of two 45 Noyes pellets per trial. In the course of the pretraining phase, the session durations decreased to about 5 min for all rats, and remained on this level during the testing period. Rats that had a total running latency of 360 sec or longer on the last pretraining day were removed from the experiments.

Training and testing were carried out during the light phase of the dark-light schedule. In general, each animal was tested every day at approximately the same time.

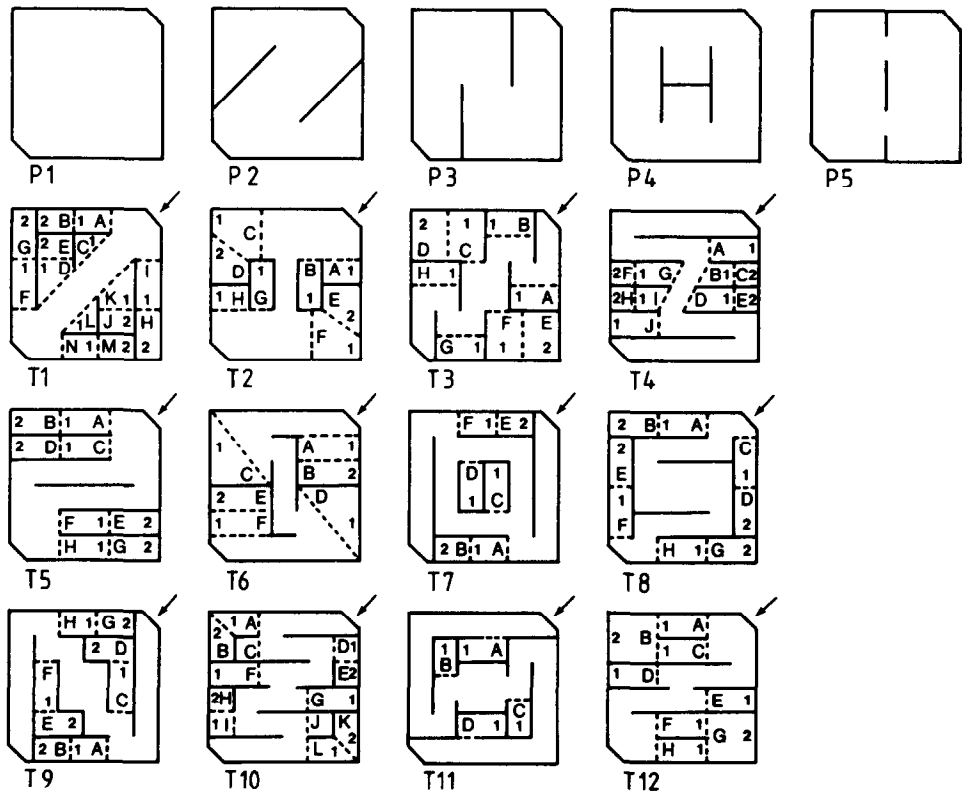


Figure 1. Pretraining and test configurations with their respective first (1) and second (2) error zones. Broken lines indicate error zone limits. The individual error zones have been marked with letters, to be referred in the text. Blind alleys are indicated with the letters of their first error zone. Arrows indicate the place where the first trial was started.

Behavioural measures

During the test sessions the route (i.e. the line indicating which error zone limits were passed with at least two paws) followed by the rat was drawn for each of the trials on maps of the configurations. When calculating error patterns from these maps, the alternating running directions were taken into account by turning half of the maps over 180 degrees.

As a conventional measure for the general difficulty level of each configuration, the total number of errors (= total number of error zones visited) per session was calculated. The spatial distribution of these errors was described by medians and 95% confidence limits (of the medians) of the number of visits to each particular error zone. In order to describe the development of the error behaviour in the course of the sessions, for each alley the number of rats per

trial visiting that alley at least once was expressed as a percentage of the total tested population (= 'pattern of initial alley visits'). As a measure of the tendency to repeat visits to alleys within trials, the percentage of rats per trial visiting an alley at least twice was also calculated (= 'pattern of repeated alley visits').

RESULTS AND DISCUSSION

Figure 2 shows that there is a considerable variation in median total error scores in the different sessions. An evident spatial differentiation of the

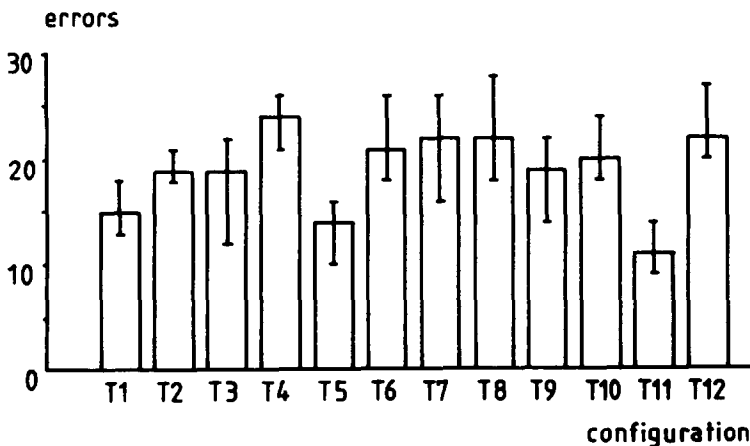


Figure 2. Medians and their 95% confidence intervals (indicated by the vertical lines) of the total number of errors per session ($n=25$).

error behaviour of the rats is shown in figure 3. The error pattern shows that in T1, T2, T5, T6, T9 and T12 there is a tendency to visit blind alleys in the vicinity of the start box more often than those near-by the goal. This tendency is less clear or absent in a number of other configurations like T3, T4, T10 or T11.

Only 4 of 64 first and 1 of 36 second error zones have a median visiting frequency of 7 or higher. Of 64 alleys 21 have median of 0 and 19 of 1 or 2. Of 36 second error zones 11 have a median of 0 and 16 of 1 or 2. Thus most of the alleys are not visited very frequently. Only a few appear to be relatively difficult as compared to the majority of blind alleys. Furthermore, rats entering a first error zone mostly also visit the second one.

Figure 4 depicts the pattern of initial alley visits, showing the changes in error behaviour within each session. Like in figure 3, baseline levels of visits differ considerably between alleys. In addition, the shapes of the learning curves of the different alleys vary considerably. Alleys with a similar total number of visits may show very different learning curves. For instance, alley B in T2 and

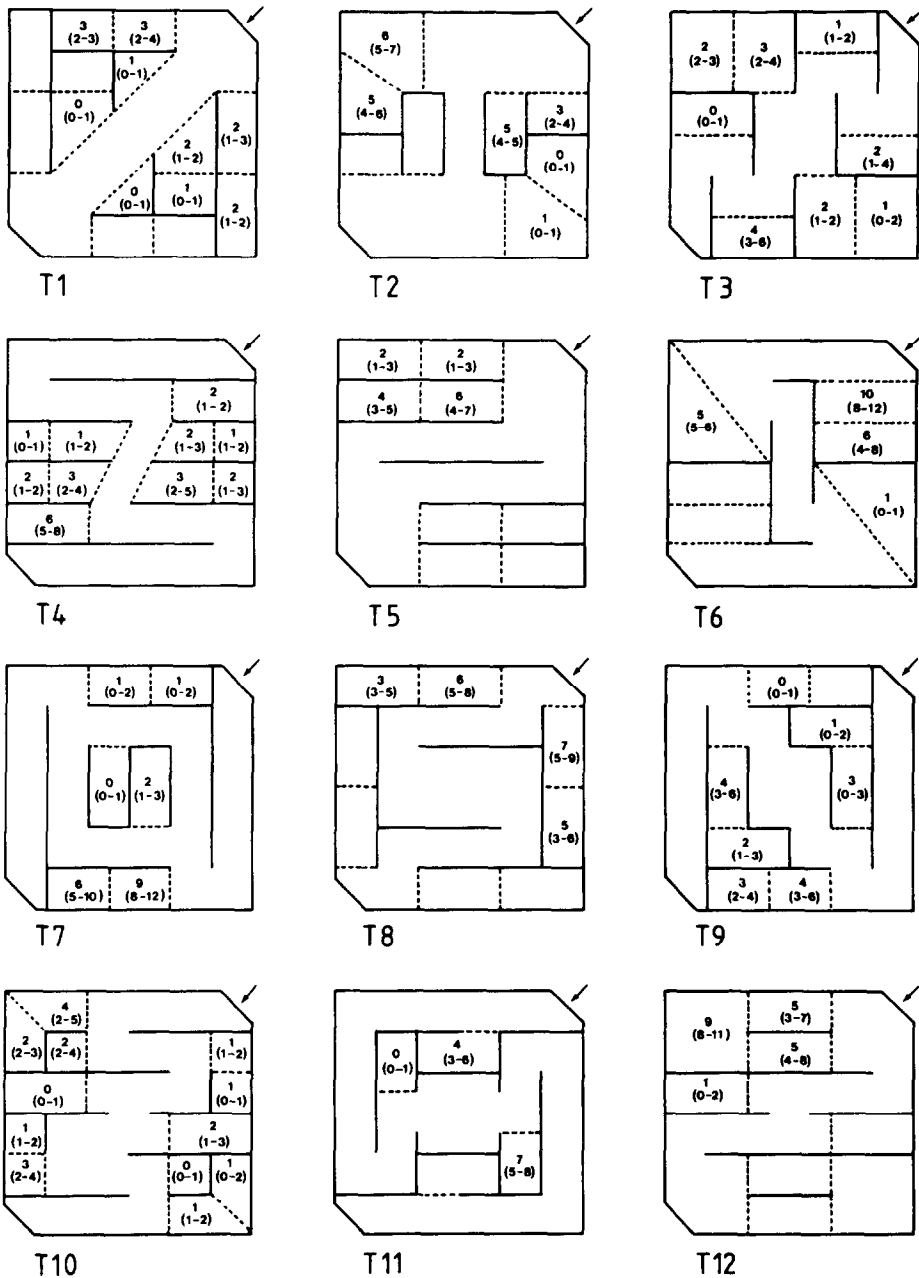


Figure 3. Spatial distribution of the medians and the corresponding 95% confidence intervals (shown between brackets) of the number of visits to each of the different error zones. Error zones with a median of 0 and a confidence interval of 0-0 were left blank. (n=25).

Figure 4. The development in the course of each of the sessions of the percentage of rats entering the blind alleys at least once (●) or at least twice (○) (n=25).

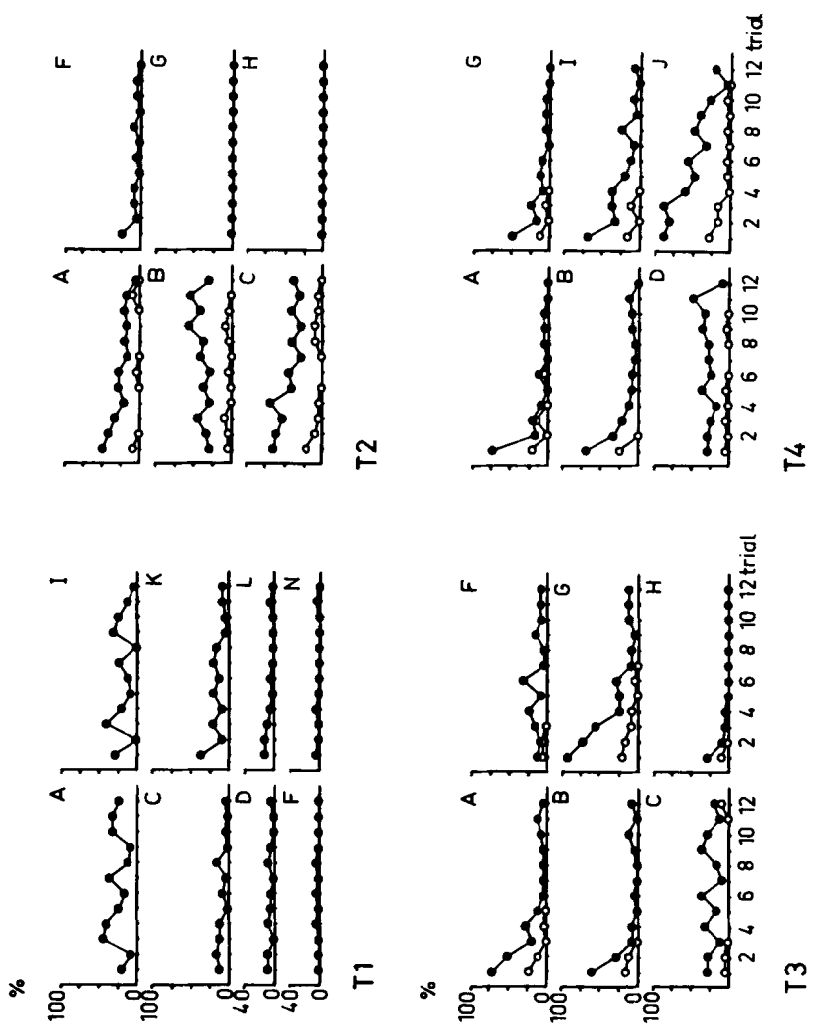


Figure 4A. Sessions 1 to 4.

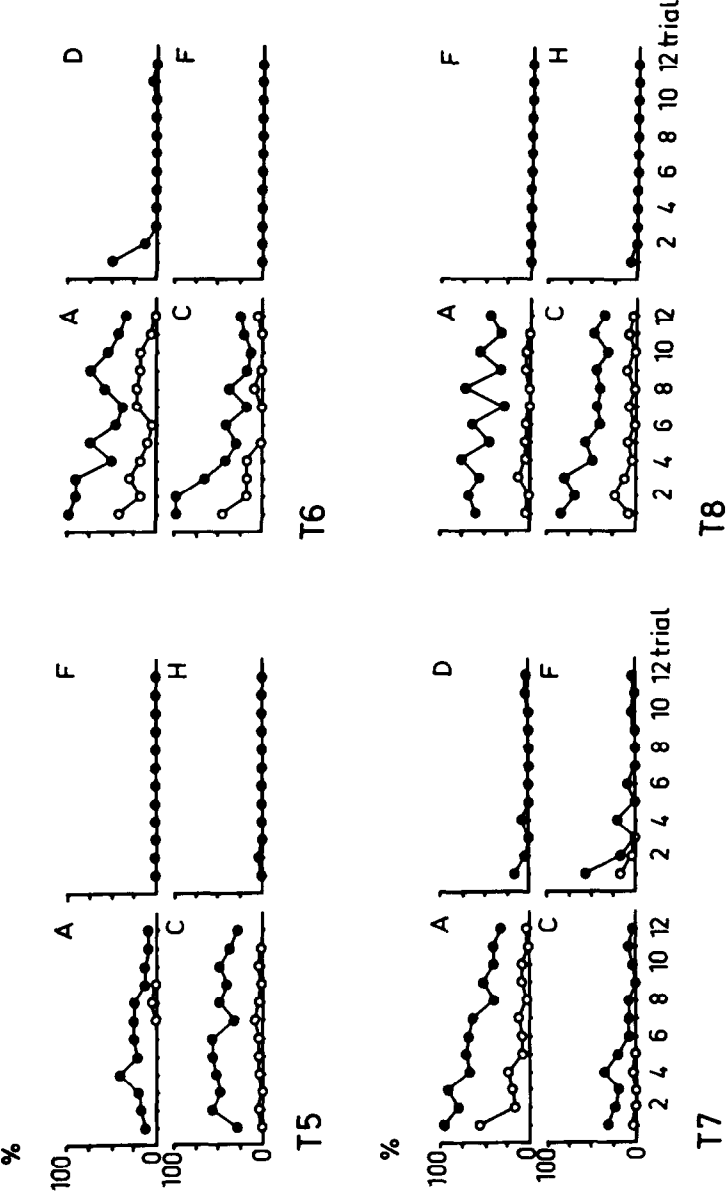


Figure 4B. Sessions 5 to 8.

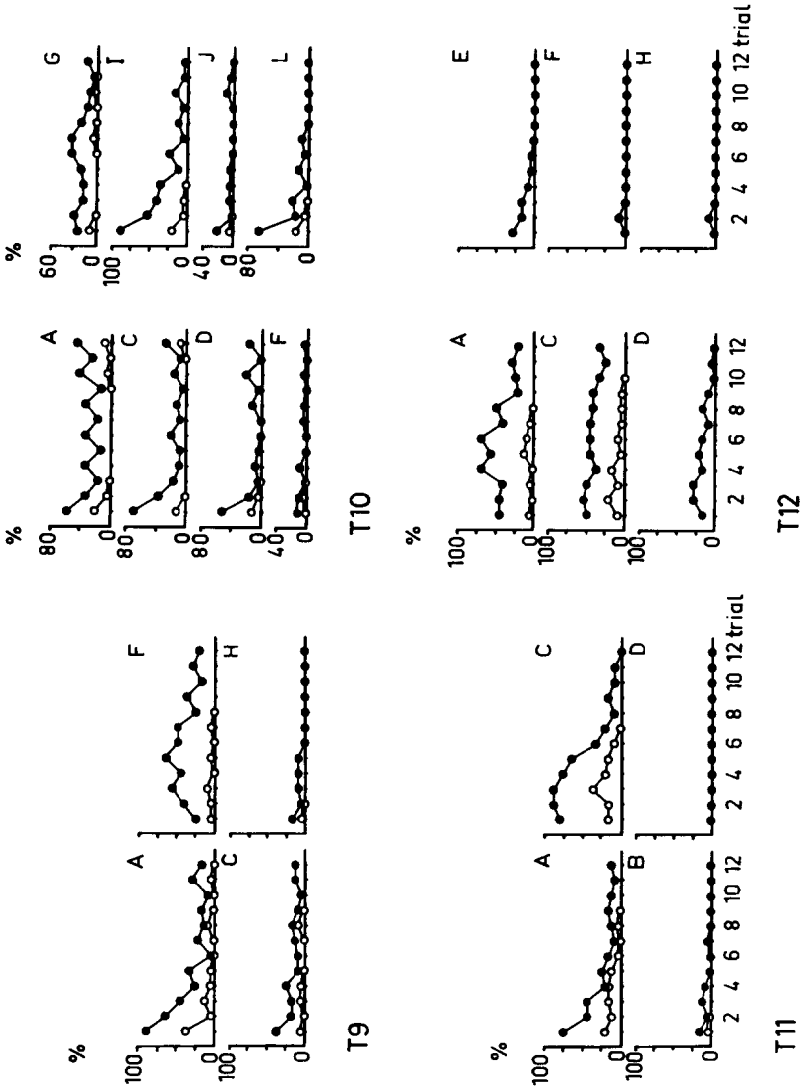


Figure 4C. Sessions 9 to 12.

alley G in T3 have a comparable median number of visits (respectively 5 and 4, see fig. 3), but totally differently shaped learning curves (see fig. 4). Error curves may decline at widely varying rates. For instance, the percentage of rats visiting alley A in T3 is comparable to that of alley C in T2. However the learning curve of the former alley does decline much faster than that of the latter one. Thus alleys with comparable initial degree of difficulty may be learned at different rates. Some curves even rise in the first few trials of the session (e.g. alley F in T9 or alley C in T11). The general picture suggests that different alleys are explored and/or learned in different ways.

The pattern of repeated alley visits (fig. 4) shows that in general the number of rats repeating visits to alleys within trials is low. The learning curves for repeated visits run more or less parallel to the corresponding curves of initial visits. Most perseverance occurs in the first trials. Only a few alleys show a relatively high perseverance. These alleys often also have high frequencies of initial visits (e.g. alley A and C in T6).

II. CORRELATIONS OF ERROR PATTERNS WITH STRUCTURAL CHARACTERISTICS OF THE BLIND ALLEYS IN THE DIFFERENT MAZES

The differences between alleys in error levels and learning curves as described in section I may be caused partly by a systematic influence of maze structure on spatial rat behaviour. Figures 3 and 4 suggest the presence of a regular relation between maze structure and the pattern of visits to blind alleys. Such a relation can be expected to result in a high correlation between structural characteristics of the maze and the number of times that rats enter the individual blind alleys. Therefore, simple geometrical characteristics of the blind alleys were selected and their correlations with a number of behavioural measures were calculated.

METHOD

The calculations were based on the data described in section I.

As dependent variables the following measures of error behaviour were used:

- 1) medians of alley visits (i.e. the median of the total number of visits per session to each of the blind alleys, they correspond to visits to first error zones), 2) pattern of initial visits (i.e. the percentage of the rats per trial visiting each alley at least once) and 3) pattern of repeated visits (i.e. the percentage of the rats per trial visiting each alley at least twice).

Four groups of independent variables were defined, further on indicated as alley characteristics, these were used as measures for a number of spatial characteristics of the blind alleys. Places in the field were expressed as coordinates ranging between (60,60) (startpoint) and (0,0) (goalpoint) (fig. 5a). The calculation of distances between places was based on these coordinates. The correct path (fig 6b) was defined as a sequence of straight lines, going from the startpoint to subsequently all corners of barriers where the rat has to make a turn, provided that the shortest route is taken.

Alley characteristics:

A. The place variables. These were measured (in cm) along the correct path (distance along the correct path preceding the alley + the shortest distance from the correct path to the mid of the entrance), or as the length of a straight line between the mid of the alley entrance and start- or goalpoint. The following variables were measured both along the correct path and along a straight line:

- Distance to start: distance of mid of alley entrance to startpoint (fig. 5c and e).
 - Distance to goal: distance of mid of alley entrance to goalpoint (fig. 5d and f).
 - Relative distance to start: distance to start as a percentage of the sum of distance to start and distance to goal.
- An additional place variable was:
- Minimal distance to goal: length of the shortest straight line between the goalpoint and the nearest point of the alley (fig. 5g).

B. The direction variables, indicating the orientation of an alley with respect to:

- the place of the goalpoint: 1 when a straight line between the mid of the alley entrance and the goalpoint crosses the alley, otherwise 0 (Direction goal, fig. 5h).
- the direction of the immediately preceding part of the correct path: when an alley can be entered by keeping the direction of the correct path immediately preceding the last turning point on that path before the alley, the distance along the correct path over which the rat runs in that direction is the score for this variable, otherwise it is 0 (Direction preceding path) (fig. 5i).
- The direction of the alley with respect to the part of the correct path immediately following the alley (Direction subsequent path). When an alley can be entered by turning too early into the direction that would be correct after passing the alley, the score for this variable is 3 when the distance between correct and nearest possible incorrect turningpoint is 0 - 5 cm, the score is 2 when the distance is 6 - 10 cm, it is 1 when the distance is 11 - 15 cm, it is 0 when the distance is larger than 15 cm or when the alley cannot be entered in this way (fig. 5j).

C. Dimensions and shape of the alley:

- Length: distance in cm from the midpoint of the entrance of the alley to the end of the alley. In the case of bent alleys two lengths are possible: the distance to the end of the first alley (ignoring the part going sideways, this length corresponds to what the rat can eventually see when entering the alley) or the distance following the bent part along its midline to the end of this part. Because it did not make a difference for the results which of these two possibilities was chosen, the mean of the two possible lengths was used (fig. 5k).
- Width: the width of the entrance in cm.
- Area: the area of the alley in cm².
- Curvature: the score is 1 for bent alleys and 0 for straight alleys. An alley is defined to be bent when part of it goes in a different direction than that perpendicular on the first error line. (fig. 5k).

D. Various other variables:

- Distance approach goal: the maximal distance over which a rat can approach the goal by entering the alley via the midpoint of the alley's entrance, calculated as the difference between 'distance to goal along a straight line' and 'minimal distance to goal' (see above).
- Total length correct path: the total length of the correct path.
- Disorientation: it is assumed that certain parts in the route may cause the rat to become disorientated. When part of the correct path has a direction that deviates at least 45° from the direction of the diagonal from startpoint to

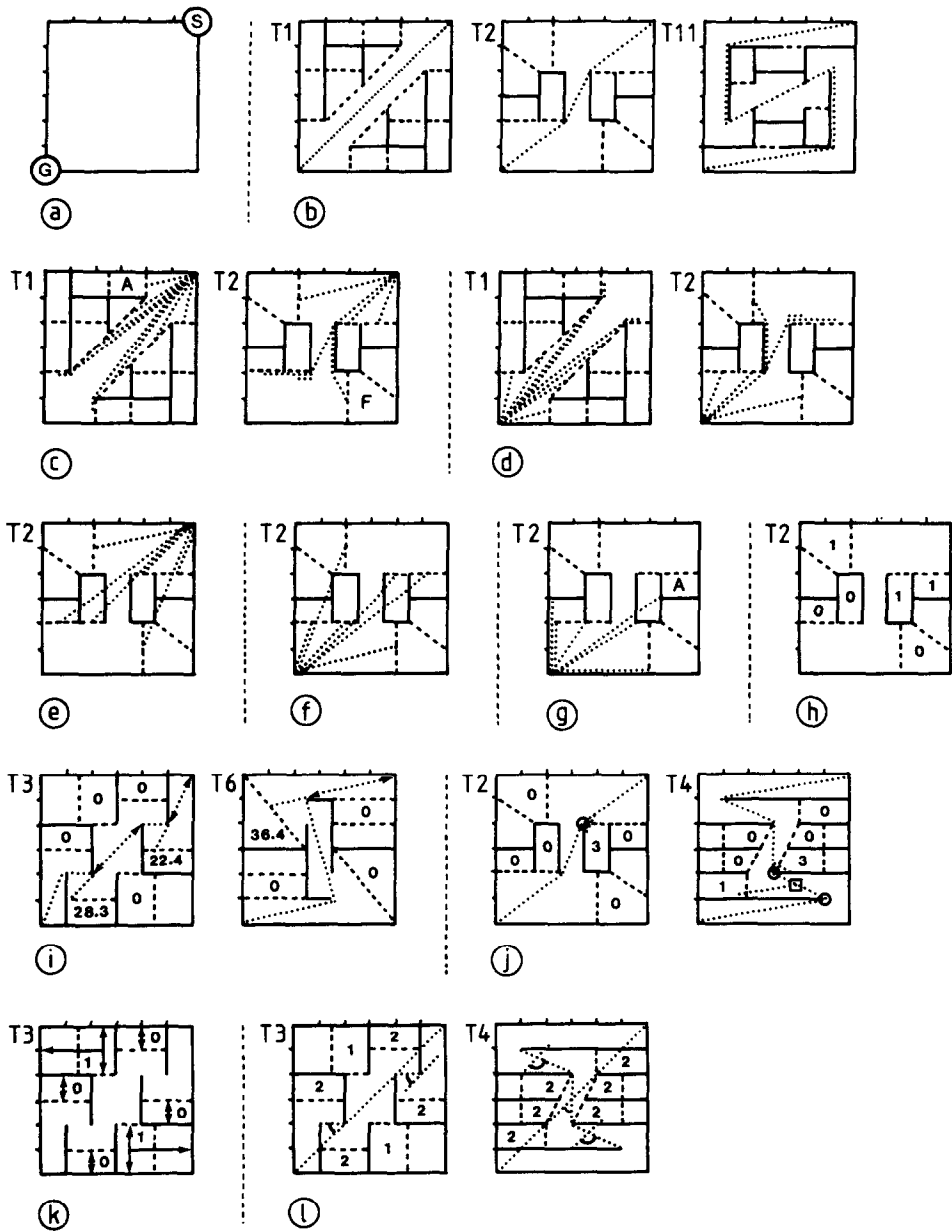


Figure 5. Examples of the way of measuring of the alley characteristics (see also method). (a) S = startpoint, G = goalpoint; (b) : correct path; (c) : distance to start measured along the correct path; (d) : distance to goal measured along the correct path; (e) : distance to start measured along a straight line; (f) : distance to goal measured along a straight line; (g) : minimal distance to goal; (h) score for direction goal; (i).....: score for direction preceding path; (j) score for direction subsequent path, O: correct turningpoint, □: incorrect turningpoint; (k) length of alley (↔) and score for curvature (number); (l) number indicates score for disorientation.

goalpoint, 'disorientation is 1 or 2, otherwise it is 0. The score 1 was given to alleys situated along a part of the correct path with a direction deviating less than 45° from that of the diagonal and 2 was given to alleys situated along a part of the correct way deviating $\geq 45^\circ$ (fig. 51).

- Testday: the number of the testday, as a measure of the general experience level of the animals.

Correlations

Pairwise correlation coefficients were calculated between all variables. Pearson correlation coefficients (r^P) were used (BM DP8D) except for variables which had only a small number of values. In these cases Spearman correlation coefficients (r^S) were calculated (BM DP3S). The critical values for $p \leq 0.05$ were used as criterion for selection of the most important correlations.

The correlations were calculated for the whole group of in total 64 alleys, and for the following subgroups: only alleys in the first or only alleys in the second halves of the routes, T1 - T6 and T7 - T12. The route subgroups were chosen because of the large differences in visiting frequency between alleys with identical dimensions and shape in the first and the second half of the routes. The testday subgroups were selected because it was of interest to compare the correlation patterns for different groups of configurations and different experience levels.

RESULTS AND DISCUSSION

Correlation of the error measures with the alley characteristics

Tables 1 and 2 show the correlations of the medians of alley visits and of the pattern of initial visits with the four groups of alley characteristics. The correlations of the pattern of repeated visits, showed a general picture comparable to that of the pattern of initial visits, although with lower correlations, and are therefore not shown.

The median number of alley visits as well as the pattern of initial visits show high correlations with the place variables. The correlations of these error measures with distances measured along the correct path are similar to or higher than those with distances measured along straight lines to startpoint and goalpoint. This suggests that the relative place of an alley along the correct path may be more important than the absolute distance to startpoint and/or goalpoint. In the first route halves the negative correlations with the distance to the startpoint (measured along the correct path) tend to be higher than the positive correlations with the distance to the goalpoint, while for the second route halves the reverse is the case. Therefore it is possible that in the first part of the route the chance to be visited is more dependent on the place of the alley with respect to the startpoint than on its place with respect to the goalpoint. The reverse holds true for the alleys in the last part of the route. The minimal distance of an alley to the goalpoint (as a measure for how close the rat can approach the goal after entering the alley) shows no strong correlations with dependent variables.

The measures of error behaviour also show significant correlations with all

Table 1. Correlations between error behaviour and three of the four groups of alley characteristics calculated for the complete group of 64 alleys. For the correlations between alley characteristics and the medians of alley visits the Pearson (p) or Spearman (s) correlation coefficients and their significance levels are shown. For the correlations between alley characteristics and the percentage of rats per trial visiting each alley at least once (i.e. pattern of initial visits), only the signs and significance levels of the correlation coefficients are shown (¹ = $p \leq 0.05$, ² = $p \leq 0.01$, ³ = $p \leq 0.001$; see method section for explanation of the variable names).

			% of rats visiting at least once												
			Medians of alley visits	Trials:											
Alley characteristics				1	2	3	4	5	6	7	8	9	10	11	12
<hr/>															
<u>Place variables:</u>															
Along correct path:															
Distance to start	(p)	-0.41 ³		-1	-1	-2	-2	-3	-3	-3	-3	-3	-3	-3	-3
Distance to goal	(p)	+0.60 ³	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3
Relative distance to start	(p)	-0.65 ³	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3
Along straight line:															
Distance to start	(p)	-0.45 ³	-2	-1	-2	-3	-3	-2	-3	-3	-3	-3	-3	-3	-3
Distance to goal	(p)	+0.47 ³	+3	+2	+2	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3
Relative distance to start	(p)	-0.47 ³	-2	-2	-2	-3	-3	-3	-3	-3	-3	-3	-3	-3	-3
Minimal distance to goal	(p)	+0.11												+1	
<hr/>															
<u>Direction variables:</u>															
Direction goal	(s)	+0.70 ³	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3
Direction preceding path	(s)	+0.16	+3	+2											
Direction subsequent path	(s)	+0.44 ³	+1	+3	+3	+3	+3	+3	+3	+2	+2	+3	+3	+2	
<hr/>															
<u>Other variables:</u>															
Distance approach goal	(p)	+0.74 ³	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3	+3
Total length correct path	(p)	+0.16	+2												
Disorientation	(s)	+0.18	+3	+1											
Testday	(p)	+0.06													

three direction variables. A high positive correlation with the direction of the alley with respect to the place of the goalpoint ('direction goal') is observed. A positive correlation between the behavioural measures and the direction of the alley compared to that of the preceding part of the correct path ('direction preceding path') is also present, but mainly in the second route halves and in

Table 2A. Correlations between error behaviour and place variables, calculated for the group of 32 alleys in only the first or only the second route halves. See table 1 for further explanation.

		% of rats visiting at least once												
		Medians of alley visits	Trials:											
Alley characteristics			1	2	3	4	5	6	7	8	9	10	11	12
<hr/>														
<u>Place variables:</u>														
Along correct path:														
First route halves:														
Distance to start	(p)	-0.42 ¹			-1	-1	-2	-1	-2	-2	-2	-3	-2	-2
Distance to goal	(p)	+0.25	+2											
Relative distance to start	(p)	-0.55 ²		-1	-3	-2	-3	-1	-2	-2	-2	-3	-2	-2
Second route halves:														
Distance to start	(p)	+0.15												
Distance to goal	(p)	+0.72 ³	+3	+3	+3	+3	+3	+3	+3	+3	+2	+3	+1	+3
Relative distance to start	(p)	-0.54 ²	-2	-2	-2	-3	-2	-2	-1	-3	-2	-2	-1	-2
Along straight line:														
First route halves:														
Distance to start	(p)	-0.12												
Distance to goal	(p)	+0.25								+1		+2		
Relative distance to start	(p)	-0.20										-1		
Second route halves:														
Distance to start	(p)	-0.28			-1									
Distance to goal	(p)	+0.20												
Relative distance to start	(p)	-0.24												

the first trials. Furthermore, mainly in the second route halves, high positive correlations are found between the error measures and the direction of the alley compared to that of the subsequent part of the correct path ('direction subsequent path'). Thus the orientation of a blind alley in relation to that of the nearest part of the correct path and in relation to the place of the goal probably affects its chance to be entered by the rats.

Furthermore, in subgroups of alleys situated in only the first or in only the second halves of the routes, there are significant positive correlations of both the medians of alley visits and the pattern of initial visits with alley length as well as alley area. Width shows positive correlations exclusively in the first trials in T1 - T6 (not shown). Curvature shows only a significant positive correlation with the medians of alley visits in the second route halves.

Therefore, the dimensions of a blind alley and possibly also its shape influence

Table 2B. Correlations between error behaviour and direction, dimension/shape and other variables, calculated for the group of 32 alleys in only the first or only the second route halves. See table 1 for further explanation.

[illegible]

its chance to be visited.

In addition, there are a number of significant correlations between the measures of error behaviour and some variables in the fourth group of alley characteristics. The distance over which a rat can approach the goal by entering the alley ('distance approach goal') shows significant positive correlations with the error measures. This indicates that the more a rat can shorten its distance to the goal by entering a blind alley, the higher is the chance that it will enter the alley. Disorientation and the total length of the correct path also correlate positively with the measures of error behaviour but predominantly in the second route halves. Therefore, possibly (especially in the second parts of the routes) a long correct path and/or parts of the correct path with a direction deviating relatively strongly from that of the diagonal between startpoint and goalpoint increase the rat's tendency to enter blind alleys.

The correlation coefficients of the pattern of initial visits in some cases show a gradient in the course of the session. Examples are the correlations of this pattern with the distance to the startpoint along the correct path, with the direction of the alley compared to that of the preceding part of the correct path, or with disorientation (table 1). This shift in correlations indicates that the relation between the blind alley characteristics and the error behaviour changes with the experience that is obtained within sessions.

The two correlation patterns based on the separate data for the configurations T1-T6 and T7-T12 (not shown), were comparable to each other and to the one described above for T1-T12. This suggests that experience acquired in previous configurations does not modify the correlations between the characteristics of an alley and its chance to be visited by a rat to a large extent.

Correlations between alley characteristics

For obvious mathematical reasons - i.e. the alleys always fit together in the same square field of fixed dimensions - there are a large number of significant correlations between the alley characteristics. We describe here only some of them. All measures in the place group except 'minimal distance to goal' correlate highly with each other. The same holds true for the variables in the dimension/shape group. Length correlates highly with area, but alley width does not. The distance over which a rat can approach the goal by entering the alley is correlated strongly with alley length and area and with the direction of the alley with respect to the place of the goalpoint. Its correlation pattern strongly resembles that of the latter variable. Disorientation and total length of the correct path also correlate strongly, probably because both increase in the case of a more or less zigzagging route. Therefore, correlations between error measures and different maze characteristics may in some cases have common causes.

In the complete group of 64 alleys testday correlates significantly with width ($r^P = -0.34$, $p \leq 0.01$), distance to start- ($r^P = +0.26$, $p \leq 0.05$) and goalpoint ($r^P = +0.26$, $p \leq 0.05$) measured along the correct path, disorientation ($r^S = +0.25$, $p \leq 0.05$) and total length of correct path ($r^P = +0.40$, $p \leq 0.01$). These correlations mean that there is a systematical change in the characteristics of the alleys in the course of the test series. Alleys wider than 10 cm occur only in T1-T6. Furthermore, test configurations in the last part of the series have longer total distances and the routes are more zigzagging. This explains the high correlation of testday with a number of other alley characteristics.

CONCLUSIONS

The characteristics of blind alleys that correlate with the rats' visiting behaviour in the mazes of the Davenport series, as suggested by the pattern of correlations found, can be summarized as follows.

- A) The place of an alley in the field along the correct path shows a high correlation with the chance of an alley to be visited. Alleys in the vicinity of the start box have a high chance to be visited, whereas for alleys in the vicinity of the goal this chance is low. Apart from a causal explanation of this gradient in the error behavior of the rats from start box to goal box, this phenomenon can be compared to the goal gradient factor, described for other types of maze (Buel, 1935; Wherry, 1941).
- B) The dimensions of a blind alley - i.e. area and/or length - and possibly its shape, form another important category of characteristics. Especially large alleys are visited more frequently than small ones.
- C) The direction of the blind alley probably also plays a role. The positive correlation of the error measures with the presence of a direction component pointing towards the goal might be related to the short cut tendency described for other mazes (Tolman et al., 1946; Tryon, 1940a). The positive correlation of the error measures with the presence of a direction component comparable to the direction of the next part of the correct path, may correspond to the anticipation tendency which has been described for other mazes (Buel, 1935; Tryon, 1940a).
- D) The distance over which the goal can be approached when entering a blind alley also shows a high correlation with the chance to be visited. When this distance is large, the alley has a relatively high chance to be visited. However, in Hebb-Williams mazes this distance is strongly dependent on area and direction with respect to the place of the goal. This means that correlation with this distance cannot be distinguished from correlations with area and direction with respect to the goal.

E) Total route length and/or the presence of parts in the correct path with a direction deviating considerably from that of the diagonal between startpoint and goalpoint correlate positively with an alley's chance to be visited. Alleys situated in mazes with a long correct way and/or with a zigzagging correct way are visited more frequently than alleys in mazes in which the route is short and has a direction corresponding approximately to that of a straight line between start box and goal box.

III. PREDICTABILITY OF ERROR PATTERNS

The high correlations between alley characteristics and the spatial distribution of errors as described in section II allow us to conclude that these alley characteristics can, at least partly, predict the error patterns. Most Davenport configurations contain relatively high numbers of small blind alleys with relatively small areas. In contrast, the areas in the Rabinovitch-Rosvold configurations are often larger, the numbers of alleys smaller, the alleys are both wide and deep and are orientated towards the goal. Accordingly, rats entering these alleys can approach the goal over a large distance. In accordance with our findings, one may expect that these alleys have high visiting frequencies and slowly declining learning curves. In order to test the predictive value of our conclusion, we studied rat error behaviour in one of the Rabinovitch-Rosvold configurations, T5 (further on called T5^R), and in two new symmetrical configurations, T20 and T30 (fig. 6). The latter two were constructed by us with the expectation that one of their alleys (alley A) would show a learning curve resembling that of the two alleys in T5^R. In addition, we constructed a more 'Davenport-like' configuration, T40, with 4 small and narrow alleys. Although the configuration is different from T9 of the Davenport series, the alleys F of both mazes (both in the second part of the zigzagging route, and with a direction resembling that of the following part of the correct path) were expected to show comparable learning curves and relatively high visiting frequencies, in spite of their large distance to the start box.

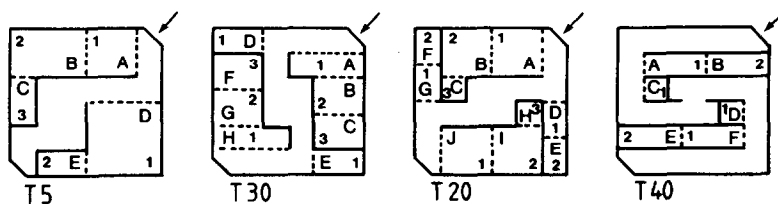


Figure 6. The structure of the configurations T5^R (T5 from the series of Rabinovitch and Rosvold, 1951), T30, T20 and T40, and their error zones.

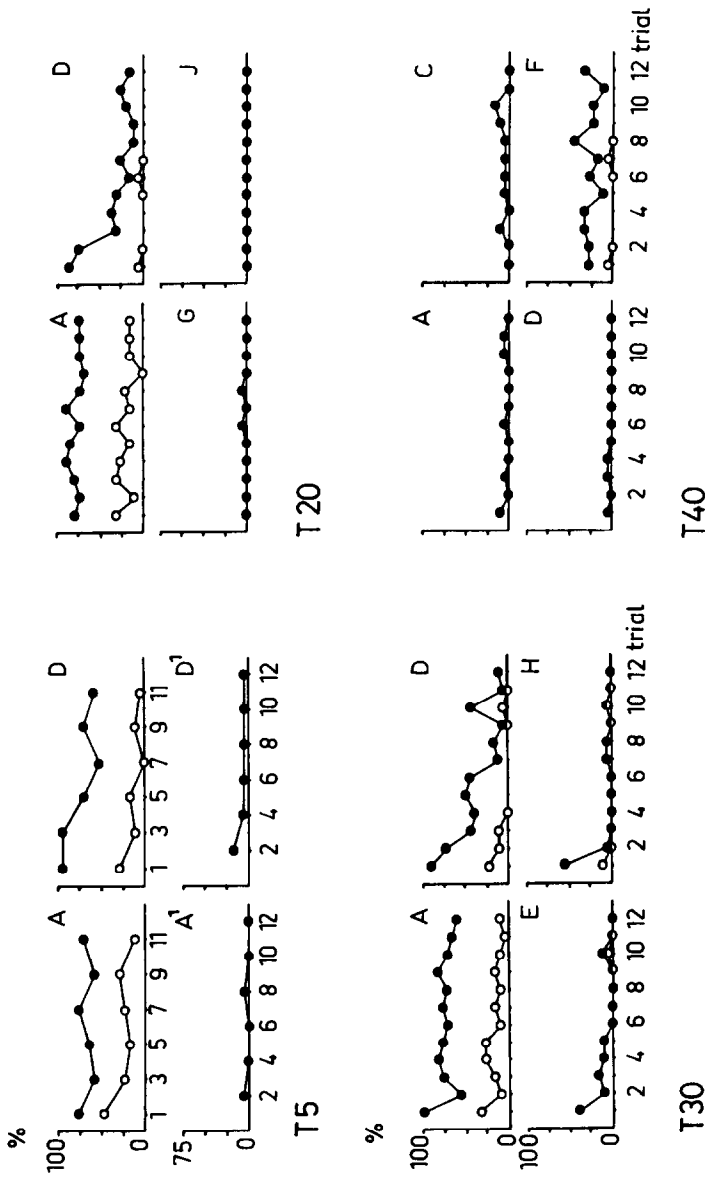


Figure 7. The alley visiting patterns in T5^R (n=17, A and D: odd trials, A' and D': even trials), T20 (n=19), T30 (n=18) and T40 (n=18). Each point indicates the percentage of tested rats that visits a blind alley at least once in a trial (●) or at least twice in a trial (○).

METHOD

Twenty male Wistar rats (body weights on the habituation day 147-187 g, approximate age 6-8 weeks) had been pretrained according to the method described in section I. After test sessions in T1, T3 and T9 of the Davenport series, the experiment was performed in two replications, testing one group 1.5 and the other 4.5 weeks later for the first time, and 4.5, respectively 2 weeks after the first test for the second time. Between the tests the animals were fed ad libitum. The day before the first test they had a pretraining session in P3, and the day before the second test they were pretrained in P4. The first test consisted of sessions in T5^R and T30, while the second test was given in T20 and T40. Half of the animals was tested first in T5^R, followed by T30, and in T20 followed by T40 (fig. 6). For the remaining group the order T30, T5^R, T40, T20 was used. Animals which refused to run in the pretraining session (2 rats in P4) or which needed more than 200 seconds to complete any test trial were dropped for that session (these were 3 rats in T5^R, 2 in T30, 1 in T40).

In spite of the above described procedural differences, the error patterns in the particular configurations showed no difference between replications. Therefore, the data of both replications were pooled. All the rats were injected with saline as described in section I.

Behavioural measures were calculated as described before.

RESULTS AND DISCUSSION

Figure 7 shows that the alleys A and D in T5^R, and alleys A in T30 and T20, as expected, show high visiting frequencies and slowly declining learning curves. The medians of alley visits to A and D in T5^R for only the six odd trials are 6 and 5, while those for alleys A in T30 and T20 (summed over 12 trials) are 12.5, respectively 12. These medians are high compared to the highest median found in the Davenport series (10 for alley A of T6, see fig. 3). Compared to the other alleys in the same configuration, alley F in T40 is the only alley visited relatively frequently, with a median of 3. Many errors made in this blind alley are probably caused by anticipation of the turn to the side of that alley that actually comes after passing it. Such an anticipation tendency is only possible after the rat has made at least one run. This may explain the increase of visits to the alley in the first few trials of the session, which is in particular obvious in T9 (fig. 4 and 7).

IV. THE EFFECT OF EXPERIENCE

Two kinds of experience may be distinguished: specific experience acquired by repeated testing in the same maze structure and aspecific experience obtained by testing in a number of different configurations. Both types of experience are expected to decrease the numbers of errors. We compared the effect of specific and aspecific experience on the error patterns of saline treated rats taken from two different experiments.

METHOD

Experiment A.

After a pretraining as described in section I, male Wistar rats (weight on the habituation day: 140 - 193 g, approximate age 6-8 weeks) were tested only on test

days 1 and 9. Between these days they were tested in T2 - T8. On each of the two test days the configurations T9 and T30 (figures 1 and 6) were used. Animals tested in one configuration on day 1 were tested in the other one on test day 9, in order to investigate the effect of aspecific experience. On day 1 19 rats were tested in T9 and 18 rats in T30 and on day 9 18 rats in T9 and 20 rats in T20.

The animals were injected 1 hour before the sessions on day 1 and day 9. Although several drug treatments were tested in this experiment, only saline treated rats were used to study the effect of aspecific experience. Because of a random re-allocation of animals over the groups on test day 9, part of the saline treated rats of this test day had been treated with drugs on day 1 (0.45 mg/kg amphetamine, 125 mg/kg beta-endorphin 2-9 or 125 mg/kg beta-endorphin 2-16). As far as we know these drugs have no long lasting after-effects on behaviour, further there were 9 non-treatment days between test days 1 and 9, and the alley visiting pattern of the rats on day 9 in T9 is comparable to that reported for saline treated rats in part I. Therefore we assume that the drug treatments on day 1 did not interact with the behaviour on day 9.

Experiment B.

Male Wistar rats (weight on the habituation day 131-149 g, approximate age 6-7 weeks) were pretrained as described before. On test day one 11 subjects had a session in T1 and 12 subjects in T9. Two days later (day 4) all animals were tested in T9.

On day 1 all animals were injected as described before with saline. On days 2 and 3 the animals were not tested, and they were fed 90 min per day at the same time as on day 1.

The alley visiting patterns in T9 and in T30 in exp A and in T9 in exp B were determined as described in section I. Effects of experience on error levels were tested with the Mann-Whitney-U test (BMDP3S). In exp A the number of errors of both groups tested on different days in the same configuration was compared. In exp B the errors of both groups on day 4 were compared to each other, and the errors of the animals trained on day 1 in T1 when tested on day 4 in T9 were compared with the errors of the other group on day 1. In exp B errors on day 1 of the group which had a session in T9 were compared to errors of the same group on day 4 with the Wilcoxon signed-ranks test (BMDP3S). These tests were all two-tailed with $\alpha = 0.05$.

RESULTS AND DISCUSSION

Effects of experience on the levels of errors

In exp A in T9 the total number of errors decreases significantly ($U = 311.0$, $p \leq 0.001$, medians and 95% confidence intervals: 43.0, 28-52 on day 1 ($n = 19$) and 20.0, 15-25 on day 9 ($n=18$)). In T30 there is also a significant decrease ($U = 342.0$, $p \leq 0.001$, medians and 95% confidence intervals: 30.5, 28-45 on day 1 ($n=18$) and 21.0, 17-24 on day 9 ($n=20$)).

In exp B on day 4 the rats with experience in T9 on day 1 display significantly lower error scores than those with experience in T1 ($U = 130.5$, $p \leq 0.001$, medians and 95% confidence intervals: 10, 7-16 ($n=12$) after T9 and: 39, 34-47 ($n=11$) after T1). In addition, they have a significantly ($p = 0.002$) decreased error score compared to their own performance on day 1 (median 43.5, 95% confidence interval 32-52, $n = 12$). The performance of the group with experience on day 1 in T1 when tested on day 4 in T9 is not significantly different from the performance of the other groups on day 1.

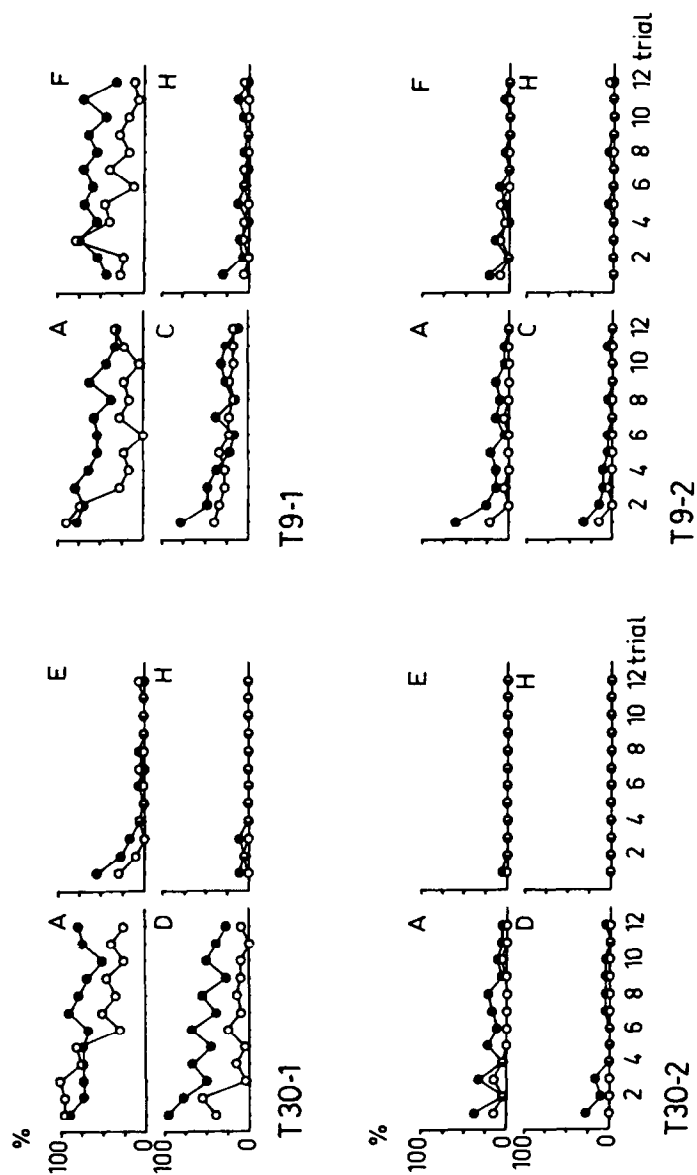


Figure 8. The effect of (aspecific) problem solving experience on the alley visiting patterns. Each point indicates the percentage of tested rats that visits a blind alley at least once in a trial (1) or at least twice in a trial (2) in configuration T30 or T9 on day 1: n=18, T9 on day 9: n=20, T30 on day 9: n=20, T9 on day 9: n=18.

Effect of experience on the alley visiting patterns

Figure 8 shows that in exp A there is a overall decrease in the percentage of rats visiting the blind alleys. In the first few trials alley A in T30 and alleys A and F in T9 have about the same percentages of visiting rats on both days. These are alleys with a strong orientation component into the direction of the goal. However, these percentages decrease faster on day 9 than on day 1, while the other alleys are visited less frequently on day 9 than on day 1 from the first trial on. Therefore, animals with aspecific experience learn faster and seem to have developed a capacity to judge immediately in the first trial that some alleys do not have a high probability to lead to the goal. Their searching seems to have become more goal-oriented.

Figure 9 shows that in exp B on day 4 the group with previous experience in T1 displays a pattern that is comparable to that of the other group on day 1. All alleys are visited by less rats from the first trial on, with the exception of alley F. The learning curve of the latter alley shows a peak in the first few trials, but this drops quickly. Thus, animals with specific experience have an almost immediately improved performance with respect to all blind alleys.

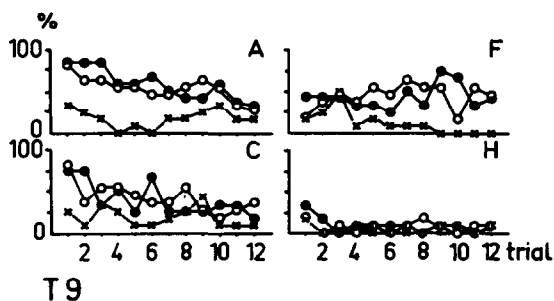


Figure 9. The effect of (specific) experience on the alley visiting patterns in T9. Each point indicates the percentage of tested rats that visits a blind alley at least once in a trial. Animals tested on day 1 in T9 (n=12): ●—●. Animals tested in T9 on day 4 after a session in T9 on day 1 (n=12): x—x. Animals tested in T9 on day 4 after a session in T1 on day 1 (n=11): ○—○.

Concluding, there seems to be a difference in the nature of the influence of specific and aspecific experience on the performance of the animals in the maze. In fact, the clearest difference between the two kinds of experience is found in the performance in the first trial. In this trial, rats with aspecific experience can only distinguish between alleys with a high and those with a low probability to lead to the goal, whereas rats with specific experience have immediately some knowledge of the actual course of the correct way.

DISCUSSION

Error behaviour and spatial characteristics of blind alleys

The data described in this paper indicate that the error behaviour of rats in Hebb-Williams mazes shows a spatial differentiation which correlates with some spatial characteristics of blind alleys. Because these characteristics can be used to predict the spatial distribution of errors of rats in other maze configurations to a certain extent, they can be helpful in developing new configurations. Systematic differences between the configurations placed early and late in the sequence of test mazes developed by Davenport et al. (1970), as well as those between configurations in the Davenport series and in the Rabinovitch-Rosvold series, can cause systematic variation in difficulty levels of these maze structures. This variation indicates that these different groups of mazes test different aspects of the maze learning ability of rats.

A limitation of our method is that the correlations of the behavioural measures with different characteristics of the blind alleys are interdependent. Experiments varying one factor at a time would be necessary to determine independent effects. In addition, the composition of the group of 64 alleys limits the factors of which influences can be shown, e.g. width did not vary enough to make a reliable determination of its effect. New experiments specifically designed for this purpose would have to be performed for the development of a more refined model.

The effect of experience

Different aspects of the effect of experience on problem solving behaviour of rats in Hebb-Williams mazes were assessed in sections II and IV.

Because it is known (Davenport et al., 1970; Rabinovitch and Rosvold, 1951) that experience in one problem solving series decreases the number of errors made in a second one, the lack of correlation found in section II between testday and error number indicates that there is an increase in the difficulty levels of the mazes in the course of the test series. Indeed, the testday was found to correlate with a number of spatial maze characteristics. Long correct path and zigzagging routes, characteristics that were found to correlate positively with visiting frequencies, occur more in the last part than in the first part of the maze series. This results in increased difficulty levels towards the end of the problem solving series.

Some of the correlation coefficients between behavioural measures and alley characteristics increase or decrease gradually in the course of the sessions. This indicates that experience acquired within sessions changes the relations between error behaviour and maze characteristics.

Concerning the performance of rats with different types of experience in the same configurations, we found that aspecific experience decreases the difficulty

level in a way different from that resulting from specific experience. Our data suggest that animals with a high experience in problem solving have developed the ability to choose immediately the most probable hypotheses of how to run in order to find the goal and adapt their behaviour quickly according to their experience with blind alleys. Animals with specific experience show knowledge of the actual course of the route from the first trial on and continue their learning of this way in the subsequent trials. However, it is necessary to be cautious to generalize this conclusion, because it is based on observations with respect to only few configurations and levels of experience.

Learning in Hebb-Williams mazes

In the habituation and pretraining sessions the animal learns the characteristics of the task that are constant, i.e the extra maze cues and some constant cues presented by the maze itself (like the wall surrounding the field and the wire mesh lid on top of the maze), the locations of the end boxes and running between these end boxes for food reward. In addition, during pretraining and testing it learns to adapt to new routes every day. In the first trial of each session, the animal can only use knowledge of the constant characteristics of the situation. The relatively high numbers of errors found in alleys oriented towards the goal, suggest that its strategy is to attempt to run directly to the known location of the goal. This discrimination between alleys orientated towards the goal and those away from it is strengthened by aspecific experience acquired in previous sessions. As soon as errors are made, the specific experience acquired through these errors is used to modify the strategy based on trial-and-error learning. This learning is facilitated by previous aspecific experience, thus the animal learns to adapt its basic strategy using new experience. This can be compared to learning set formation: 'learning to learn' (Whishaw, 1985).

Actually, although the procedure is called a problem solving test, a great deal of learning seems to be trial-and-error learning. There is not any strategy which could theoretically lead to immediately errorless behavior in each configuration. In contrast to the original series of Hebb and Williams (Hebb and Williams, 1946; Hebb, 1947), most of the problems in the series of Rabinovitch and Rosvold (1951) and Davenport et al. (1970) cannot be solved by visual discrimination between blind and open alleys. Moreover, the error patterns do not support the assumption that the rats tend to adopt such a strategy. It cannot be excluded that a tendency to run straightly to the goal exists already in untrained rats, and that this pre-existing strategy is only strengthened in pretraining and testing. Therefore, efficient performance in this test can be described as a first selection of alleys based on constant environmental cues which indicate the location of the goal, and on spatial characteristics of the alleys (probably

especially their place and direction), followed by further selection through fast trial-and-error learning.

A nowadays more commonly used spatial test, in which rat behaviour has been investigated into great detail, is the radial maze (Olton, 1978). A comparison between this test and the Hebb-Williams test is of interest in order to see whether they measure similar or different capacities in rats.

First of all, part of the task in each test is identical for all sessions: visit all rewarded arms in the radial maze, and run to the goal box in the Hebb-Williams maze. In addition, part of both tasks changes between sessions (remembering the arms visited or not yet visited in the radial maze and learning the new route in the Hebb-Williams maze).

Secondly, the routes from the platform to the rewards are always simple, straight and constant between sessions in the radial maze. In the Hebb-Williams maze, however, the routes are often complicated, zigzagging and different between sessions. Accordingly, there are differences between the two maze tests with respect to the kinds of information that the rat has to learn.

Thirdly, the number of rewarded places is in general larger in the radial maze (usually 8 or more) than in the Hebb-Williams test (only 2).

Fourthly, extra maze cues from the constant environment can be used in both tests. Rats tend strongly to use extramaze cues in the radial maze (Olton and Samuelson, 1976). However, the Hebb-Williams test offers more opportunity to use intramaze cues, because the alleys are not equally shaped and spaced unlike the arms of the radial maze. In a Hebb-Williams maze, extra maze cues can also be used by a rat to determine its actual location in space at a certain moment and the locations of the end boxes, but obviously these cues cannot serve to find the correct route in a first run. However, they may be used in the trial-and-error learning process. The spatial error pattern could partly be the result of interaction of spatial alley characteristics and orientation on extramaze cues. The contribution of direction variables and perhaps partly the error gradient from start to goal may be explained in this way. Other correlations suggest that intramaze cues, e.g. shape and area of an alley, also play a role in learning Hebb-Williams mazes.

Fifth, in the radial maze test a rat has to visit as many different arms as possible. The optimal behaviour may already be reached in the first few trials that the animals runs in the maze, only by showing the species-specific exploration and alternation tendency. Rats often perform above chance level from the very first trial on. This is an important difference with the Hebb-Williams test. Here the rats need a relatively extensive pretraining in order to learn the general task. A rat exploring all alleys in a Hebb-Williams maze makes many

errors, thus for optimal performance the animal has to learn to suppress this tendency.

Sixth, the variable part of the information learned in the Hebb-Williams maze does not have the short-term character of the memory for arms visited in the radial maze (Markowska et al, 1983), it is remembered very well for at least two days.

Concluding, the two tasks do not test identical aspects of spatial learning capacity in the rat. Basically, the radial maze task tests the capacity to learn and remember a number of places while the Hebb-Williams task tests the capacity to find and learn a route.

The analysis of treatment effects

Effects of pharmacological treatments or brain lesions on the total numbers of errors in Hebb-Williams mazes do not necessarily reflect the essential changes in error behaviour. Some examples of conceivable changes of error patterns and their interpretations can be mentioned. Firstly, the orientation on extra maze cues or the capacity to locate places in space may be affected. The correlation of error patterns with direction and possibly place variables can then be changed. The animals may shift their attention from outside to inside cues, increasing the effect of intramaze cues. Secondly, learning set formation may be affected. The effect of aspecific experience will then change and therefore the initial selection (in the first trial) of alleys and the rate of error and trial learning. Thirdly, exploration may be increased, resulting in a decrease of the correlation of error patterns with place and direction variables. The influence of shape/dimension variables may increase. Fourthly, in case of a changed motivation to find the goal, the goal-directedness of the error patterns can be expected to change. The contribution of direction variables may decrease. The animals may behave more explorative, but may in addition have a higher tendency to stay close to the start, leading to a stronger relation of error patterns with place variables. Accordingly, knowledge of basic error patterns and their change can be used in understanding the nature of the effects that various kinds of treatment may have on Hebb-Williams problem solving scores.

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